THE FOLIAR SCLEREIDS OF TROCHODENDRON ARALIOIDES SIEB. & ZUCC.

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With four plates

INTRODUCTION

THE PRESENCE of branched sclereids in the parenchyma of the foliage leaf of *Trochodendron* has been regarded by Blenk (5), Matsuda (8), Parmentier (9, 10), Harms (7), van Tieghem (13), and Solereder (12) as one of the important diagnostic characters of this remarkable dicotyledon. As far as I have been able to determine, however, no study has been made either of the structure and development of the sclereids or of the possible fluctuations in their relative abundance, form, and distribution within the leaves of different individuals. Data on these points are essential in any effort to judge the systematic value of the sclereids in differentiating *Trochodendron* from other woody ranalian genera. In the present article, the results of a study of the form, structure, and distribution of sclereids in the mature foliage leaf of *Trochodendron* are presented. Living material, as well as leaves from 25 separate herbarium collections, has been investigated. A study of the ontogeny of the sclereids is now in progress and the results will be described separately in a future paper.

MATERIAL AND METHODS

Abundant fresh material was secured, through the coöperation of Mr. Eric Walther, from a vigorous specimen of *Trochodendron* growing in the Strybing Arboretum of Golden Gate Park, San Francisco. Professor I. W. Bailey kindly furnished leaves from 20 herbarium collections representing. in equal number, specimens collected at various localities in Japan and Formosa. Acknowledgement is also due to Miss Alice Eastwood of the California Academy of Sciences, Dr. J. M. Greenman of the Missouri Botanical Garden, and Dr. H. L. Mason of the University of California for providing additional herbarium material from Japan. Specific reference to the various herbarium sheets is made in the text as well as in the explanatory legends accompanying the plates.

In order to study the form and distribution of the sclereids in the lamina of herbarium specimens, the general technique recently outlined by Bailey and Nast (1: 472–473) was employed. Sectors of the lamina, extending from the margin to the midrib, were first heated in water, then cleared in an electric oven in 5% NaOH, dehydrated in alcohol, and mounted from xylene without staining into balsam. Fresh material was similarly processed except that it was found desirable to extract first the chlorophyll in hot alcohol. For a more detailed examination of the form of the sclereids. portions of the lamina and petiole of fresh leaves were macerated by the

method already described in a recent article (Foster 6: 303–304). Serial sections of both the petiole and sectors of the lamina of fresh leaves were also studied and were prepared by the usual technique (Foster 6: 303).

Grateful acknowledgement is made to my wife, Helen Vincent Foster, for her skillful drawings of the sclereids illustrated in *Plates II-IV*, and to Professor I. W. Bailey for his helpful comments throughout the investigation.

DISTRIBUTION OF THE SCLEREIDS

Before describing the remarkable polymorphism of the foliar sclereids, it is necessary to comment briefly on the general distribution of these cells in the adult foliage leaf. Serial sections as well as cleared leaf-sectors show that the sclereids typically occur as idioblasts dispersed through certain of the parenchymatous tissues of both petiole and lamina. In the petiole, the sclereids are most abundant in the inner extremely lacunate region of the cortex. Longisections indicate that, while the sclereids may occasionally appear in superposed groups of three or more connected cells, they are usually isolated from one another by parenchymatous elements. In the lamina, sclereids are found as idioblasts in the parenchyma tissue of the midrib and throughout the spongy mesophyll to within a few cells of the marginal epidermis. A careful study of cleared laminar sectors reveals considerable fluctuation in the relative abundance of sclereids. In many of the Japanese and Formosan collections, the profusely branched sclereids are so crowded as to suggest a loose "tissue" (*fig. 2*), while in other specimens, as for example G. G. P.[1], the sclereids tend to be more widely and evenly spaced within the vein-islets (*fig. 1*). Several of the Formosan collections appear unique because of the presence of small nests or clusters of irregular thick-walled sclereids above the juncture of the veins supplying each marginal tooth. This structural peculiarity is entirely wanting in the G. G. P. and the Japanese collections which have been studied and cannot be properly interpreted until a wider range of material is available for examination.

FORM AND STRUCTURE OF THE LAMINAR SCLEREIDS

Previous descriptions of the sclereids of *Trochodendron* are both vague and inadequate and, as in the case of the sclereids of *Camellia japonica* (Foster, 6), a variety of terms has been applied to these cells, viz.: (1) "branched sclerenchyma cells" (Blenk, 5; Prantl, 11; Harms, 7; Solereder, 12); (2) "sclérites"[2] (van Tieghem, 13); (3) "internal hairs"[2] (Parmentier, 9, 10), and (4) "trichoblasts"[2] (Matsuda, 8). In none of these

[1]For brevity, the abbreviation "G.G.P." will be used throughout this paper to refer to the leaves of the specimen in Golden Gate Park, San Francisco.

[2]This term and others which have been applied to idioblastic sclereids in the seed plants have been discussed historically in a recent paper (Foster, 6). In that article (Table 1, p. 320) Seward is incorrectly cited as the originator of the term "sclérite." Further research shows that this term can be traced back through the French literature as far as the work of Bertrand (4). It has not been possible, however, to determine whether this author was the first to introduce the term into botanical literature.

papers, however, is any indication made of the remarkable polymorphism of the sclereids which is only fully revealed by the study of cleared sectors taken from comparable regions of the lamina of different individuals. By means of this relatively simple technique it becomes obvious that the laminar sclereids vary from radiately branched elements with dichotomous arms (*figs. 7–11*) to bizarre asymmetrical (*figs. 12, 13*), cruciform (*fig. 14*), and fiber-like forms (*figs. 15–22*). Intergradations of the most varied character occur between these form-types and preclude rigid demarcations. Nevertheless, when the *extremes* in sclereid-form are studied from the standpoint of their frequency and location within the lamina, certain interesting trends can be detected. The profusely ramified type of cell (*figs. 7–13*) appears to dominate throughout the submarginal portion of the laminae of all collections. In contrast, the strictly fusiform type of sclereid (*figs. 16–22*) attains the peak of development in the marginal portion[3] of the lamina and, moreover, is most consistently present in the leaves of the Formosan collections. Indeed, during the early phases of the investigation it seemed possible that the presence of large fiber-like marginal sclereids might represent a unique feature restricted to the leaves of Formosan plants. The examination of additional herbarium material from both Japan and Formosa, however, failed to reveal a sharp contrast with respect to this feature. For convenience, the fusiform and ramified types of sclereids will be described separately with special reference to (1) their occurrence within the various collections and (2) their form and structure.

1. *Fusiform types.* On the basis of the herbarium specimens available for study, it is clear that the fusiform or fiber-like type of sclereid is most abundant and reaches its greatest size[4] in the marginal region of the lamina of the Formosan collections (*figs. 2, 16–19*). Out of ten separate collections, only two failed to exhibit this character plainly. In contrast, the marginal sclereids in the collections from Japan tend to be profusely ramified and in many specimens differ from the submarginal sclereids merely in their larger size and more massive walls. Several of the Japanese collections were particularly notable for the complete absence of contrast, either in size or form, between the marginal and submarginal sclereids (e.g. *Wilson 6041*). Five out of the fifteen Japanese collections, however, were exceptional. One of the most striking of these was represented by the leaves of seedlings collected on Yakushima. In this material, long, slender, fusiform elements with abundant spicules are common in the marginal region of the lamina (*fig. 20*). Several other Japanese collections were likewise distinguished by the presence of fusiform marginal sclereids (*figs. 21, 22*). But in these specimens the sclereids are much shorter and less fiber-like than in the extreme examples provided by the Formosan material.

[3]By "marginal" is meant the narrow border of tissue between the small peripheral veins and the marginal epidermis. "Submarginal" designates the remaining portion of the lamina exclusive of the midrib (cf. *fig. 1* and *2*).

[4]The length of the fiber-like sclereids represented in *figures 16–19* are, respectively: 763, 795, 588, and 602 microns.

Structurally regarded, the fusiform type of marginal sclereid is very thick-walled with the lumen reduced to a narrow channel except in the median region of the cell. In certain of the Formosan collections (*Henry 1398, Simada 350, Tanaka 5412*) many of the fiber-like sclereids are relatively smooth-walled except near the mid-region (*figs. 16–18*). More commonly, however, the sclereid is provided with very numerous sharp-pointed spicules or blunt, knob-like processes (*figs. 2, 19, 21, 22*). This condition closely resembles the situation in the large fusiform petiolar sclereids of *Camellia japonica* (Foster 6, *pl. 2* and *3*). In contrast, however, to the extremely numerous and often ramiform pit-canals typical of the sclereids of *Camellia,* pits are relatively few and apparently are restricted to the central portion of the fusiform sclereids in *Trochodendron.* A full discussion of their structure and development will be presented in a future paper.

2. *Ramified types.* As stated earlier in this paper, the ramified type of sclereid predominates throughout the submarginal region of the lamina of all collections (*figs. 1, 2*). Branched sclereids, which fluctuate greatly in size, also occur interspersed among the huge fiber-shaped marginal sclereids of the Formosan collections (*fig. 2*). In this material, transitions between fusiform and branched types are abundant and often are extremely irregular and grotesque in character (*fig. 18*).

As is clearly shown in *Plate III,* the branched sclereids vary widely in their form. In certain of the collections from Japan as well as Formosa a series of repeatedly dichotomizing branches radiates in a more or less symmetrical fashion from the central body of the sclereid (*figs. 7, 9*). More commonly, however, the branched sclereids are asymmetrical because of the unequal development of one or more of the arms (*figs. 1, 2, 8, 10–13*). There is, of course, no sharp boundary between the symmetrical and asymmetrical types of branching and both conditions may intergrade within the same leaf. The forms depicted in *Plate III* were deliberately selected to show some of the extremes. In one collection from Japan an amazing degree of polymorphism was discovered, the sclereids ranging in form from profusely branched elements to cruciform and short, irregular, fiber-like types (*figs. 14, 15*). In no other specimen investigated were submarginal sclereids, comparable to the cell shown in *figure 15,* encountered.

As to structure, the ramified sclereids typically are thick-walled cells with correspondingly narrow lumina (*figs. 8–13*). Exceptions to this condition, however, occur in two collections, one from Japan (*Siebold*) and one from Formosa (*Tanaka 5412*). In these specimens, *all* of the submarginal sclereids are relatively thin-walled and possess very slender arms (*fig. 7*). Some of the Japanese collections exhibit an extreme condition with respect to the thickness of the sclereid-wall. In these cases, a "stratum" of very thin-walled sclereids occurs just beneath the abaxial epidermis. Many of these cells are trilobate in surface view and differ from the neighboring parenchyma elements principally by the presence of very short, spicule-like arms. The latter may occur in pairs at each corner or may be unequal in number and vestigial in appearance. Such sclereids, in a certain sense,

seem to represent transitions between parenchyma cells and the more elaborately branched, thicker-walled sclereids which occur at deeper levels in the mesophyll. The relative abundance of spicules on the ramified types of sclereids fluctuates widely. For example, spicules appear consistently on all the sclereids of the G. G. P. specimen, their abundance varying with the size and form of the cell (*figs. 1, 5, 6, 8*). Spicules are likewise prominent in one of the collections from Yakushima, Japan (*fig. 13*). Beginning with these extremes, various conditions of decreasing prominence of spicules were noted in the collections culminating in such smooth-walled types as is illustrated in *figure 7*. As in the case of the fiber-like marginal sclereids, pits are few in number and are confined to the median region of the cell.

FORM AND STRUCTURE OF THE PETIOLAR SCLEREIDS

As stated previously, sclereids are largely confined to the inner highly lacunate cortical parenchyma of the petiole. The examination of partially macerated tissue, supplemented by serial longisections, of the G. G. P. specimen reveals extensive fluctuations in the form of the petiolar sclereids. In no instance, however, have symmetrical radiately branched elements comparable to those found in the submarginal portion of the lamina been observed. Very commonly, the petiolar sclereids are roughly H-shaped, with paired, acuminate vertical arms (*fig. 3*). The latter lie freely within the longitudinally extended air-spaces in the parenchyma. In elements of this type, one or more uncinate lateral branches are often present. Further complexity results in many cases from the development of additional vertical arms (*fig. 4*). Sclereids of this kind likewise are scattered within the parenchyma tissue of the midrib. Many of the petiolar sclereids, however, are more irregular in form, with their various branches unequal in length and radiating in the most varied directions from the central body. As shown in *figures 3* and *4* spicules, varying in size and distribution, occur in the petiolar sclereids.

Because of the great difficulties involved in the study of cleared portions of the petiole, it has not been possible to determine fully the distribution of the various form-types in the herbarium collections. However, in several of the Formosan collections (*Simada 350* and *Wilson 11231*) magnificent examples of fiber-like sclereids occur in addition to H-shaped and irregularly branched types. Two of the longest of the fusiform types measured respectively 1002 and 1465 microns in length. Such extremely long sclereids are of particular interest because of the presence of similar but shorter cells in the marginal region of the lamina of the same specimens (cf. *figs. 17* and *19*). Whether typical fiber-like sclereids ever occur in the petiole of the Japanese material remains to be determined. As far as the present study goes, there is no evidence of them.

DISCUSSION AND CONCLUSIONS

The present study of the foliar sclereids in *Trochodendron* provides an excellent illustration of the range in form, size, and structure possible within

the limits of one morphological "cell-type." Because of the abundance of intergradations it is obvious that no sharp boundaries exist between the various form-types. Thus, in the lamina, the profusely branched and fiber-like forms are clearly the extremes in cell specialization at the two ends of a continuous morphological series (*Plates III* and *IV*). Similarly, in the petiole, the H-shaped and fusiform types cannot be rigidly demarcated from the more irregularly branched forms.

From these facts it is clear that the entire gamut of form-types must be fully recognized if the sclereids are to be used as one of the diagnostic criteria of *Trochodendron*. This is particularly evident when the fluctuations in the occurrence of the fiber-like type of sclereid are taken into consideration. In the majority of the Japanese collections, strictly fusiform, unbranched sclereids are absent from both the marginal and submarginal portions of the lamina. Conversely, the majority of the Formosan specimens are distinguished by the high proportion of elongated, relatively unbranched, marginal sclereids (*figs. 2, 16, 17, 19*).

Admittedly, however, the present investigation has merely uncovered what appears to be a *general trend* in the distribution of the fiber-like type of foliar sclereid. Obviously a wide range of leaf-types, collected from different regions of the same plant as well as from individuals growing under various ecological conditions in both Japan and Formosa, should be compared. Nevertheless, in the material examined, there appears to be no correlation between the size or form of the lamina and the presence or absence of fiber-like marginal sclereids. This is most convincingly shown in the case of the living specimen in Golden Gate Park. Here it was possible to examine a wide series of leaf-types, including the minute laminae of the transition forms between bud-scales and foliage leaves. In all instances, the marginal region of the lamina is devoid of the very elongate, fiber-like sclereids typical of most of the Formosan collections (compare *figs. 1* and *2*). The herbarium material was necessarily very limited and consisted of one or two leaves from each collection. Nevertheless the size and form of the leaf varied and, in the specimens furnished by Professor Bailey, included laminae which were lanceolate, ovate, and rhomboid in contour (cf. Bailey and Nast, 3: *Pl. V*). In all of this material, the occurrence of fiber-like marginal sclereids varied independently of either the size or form of the leaf-blade.

In their recent survey of the leaves of the Winteraceae, Bailey and Nast (2) have shown that the trends of sclerification include armed sclereids as well as nests of sclereids, lignified thickenings of the mesophyll, and sclerenchymatous vein-jackets. In *Trochodendron*, whose systematic relationships with other ranalian groups remains to be clarified, the foliar sclereids appear to exhibit two major trends in specialization, viz.: (1) the slender, radiately branched types (*figs. 7–11*) and (2) the massive fiber-like forms (*figs. 16–22*). The phylogenetic and systematic implications of this polymorphism will not become apparent, however, until the foliar sclerenchyma of other ranalian genera has been fully studied.

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EXPLANATION OF PLATES

PLATE I

Laminar sectors cleared in NaOH and photographed unstained in balsam. In each figure, the margin is toward the upper edge of the plate. Magnification × 93.

FIG. 1. Golden Gate Park material, showing irregularly branched sclereids. Note the large size and muricate surface of certain of the marginal sclereids. FIG. 2. *Simada 876,* Formosa, showing the closely packed fiber-like marginal sclereids. Note variations in size and type of branching of the submarginal sclereids.

PLATE II

Camera-lucida drawings of sclereids isolated by maceration from leaves of the Golden Gate Park specimen. In order to show the distribution of the spicules, the narrow branched lumen of these cells has been omitted in the drawings. Magnification × 240.

FIG. 3. Slender H-shaped sclereid from the petiole. Note the short uncinate branches of this cell. FIG. 4. Sclereid from the petiole with three systems of vertical branches. Note intergradations between spicules and short lateral branches. FIG. 5. Radiately branched sclereid from the submarginal region of the lamina. FIG. 6. Large, irregularly branched, muricate sclereid from the marginal region of the lamina. Elements of this type are also shown *in situ* in *Plate I, fig. 1.*

PLATE III

Camera-lucida drawings of sclereids from the submarginal region of cleared sectors of the lamina. Each cell is shown as it appears in median optical view; the central portion of the lumen is indicated by the broken outline. *Figs. 7–11,* radiately branched types; *figs. 12, 13,* irregularly branched types; *fig. 14,* cruciform type; *fig. 15,* irregular fiber-like type. Magnification × 180.

FIG. 7. *Siebold* (type coll.), Japan. FIG. 8. *Golden Gate Park* specimen. FIG. 9. *Wilson 11231,* Formosa. FIG. 10. *Wilson 11231,* Formosa. FIG. 11. *Sasaki 351,* Formosa. FIG. 12. *Henry 1398,* Formosa. FIG. 13. *Wilson 6041,* Yakushima, Japan. FIG. 14. *U.S.N.H. 350937,* Japan (*Collector?,* May 25, 1897, Amagi-san). FIG. 15. *U.S.N.H. 350937,* Japan (*Collector?,* May 25, 1897, Amagi-san).

PLATE IV

Camera-lucida drawings of fiber-like sclereids from the marginal region of cleared sectors of the lamina. Each cell drawn in median optical view; dotted outline indicates central portion of lumen. Magnification × 180.

FIG. 16. *Henry 1398,* Formosa. Long, slender, fiber-shaped sclereid. Note relatively smooth wall. FIG. 17. *Simada 350,* Formosa. Note short, irregular branches near central region of cell. FIG. 18. *Tanaka 5412,* Formosa. Irregular, fiber-like sclereid. This cell illustrates the common intergradation in form between strictly fusiform and branched sclereid-types. FIG. 19. *Wilson 11231,* Formosa. Very broad, fusiform type, prominently muricate. Consistently present in this collection. FIG. 20. *Wilson 6041,* Yakushima, Japan. Fiber-like type, with abundant spicules. FIG. 21. *Jack,* Oct. 25, 1905, Japan. Short, fusiform type. Abundant in this collection. FIG. 22. *U.S.N.H. 350937* (*Collector?,* May 25, 1897, Amagi-san). Short, irregularly branched type, closely resembling *fig. 21.*

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